



Meta-analysis of the effect of global warming on local species richness

Abstract

We carried out a systematic review of global and regional modelling studies in which shifts in species distributions under climate change were modelled. These studies included a large range of species groups and biomes worldwide. Based on the model results we calculated the fraction of species that would remain at a locality in response to projected climate change and related this to the global mean temperature increase (GMTI) that was associated with projected climate change. Out of 207 articles meeting our search terms used in Web of Science, 21 studies met our selection criteria and were included. This resulted in 239 data points of combinations of global mean temperature increase and effect on local species richness across different species groups and biomes. Based on this we carried out a meta-analysis to investigate the relation between changes in global mean temperature increase and the fraction of remaining plant and vertebrate species at a geographic location. The results showed that global mean temperature increases of more than 2°C above pre-industrial levels significantly affect local species richness. Both plants and vertebrate species showed a strong decline in the fraction remaining species with increasing temperature. The effect impacts seemed to be strongest in warm biomes and tended to be smaller in cool biomes. The resulting meta-model can be used to calculate the fraction of remaining species under different climate change scenarios.

Introduction

Over the past two centuries human activities have dramatically increased atmospheric concentrations of green

house gasses, resulting in rising global surface temperatures and changing precipitation patterns (IPCC, 2013). Habitat loss and climate change constitute the greatest threats to biodiversity worldwide over the next century (Alkemade *et al.*, 2009; Parmesan & Yohe, 2003; Sala *et al.*, 2000b; Warren *et al.*, 2011) and are likely to alter ecosystem processes and reduce ecosystem resilience to additional or continued negative pressures (Chapin *et al.*, 2000). Where habitat loss generally results in instant loss of biodiversity, the effect of climate change is expected to result in a more gradual deterioration of habitat suitability, potentially creating an 'extinction debt' (e.g. Bertrand *et al.*, 2011; Tilman *et al.*, 1994) in which responses of species show delay before they manifest themselves.

A mean annual temperature increase of 3 °C at a specific place roughly corresponds with temperatures normally found approximately 300 to 400 km southwards (northern hemisphere) or 500 m downward in altitude (Hughes, 2000), with species getting more likely to go locally extinct in the equatorward extent of their range (i.e. the southern extent of their range at the Northern hemisphere) and potentially expanding their range poleward. For instance Schippers *et al.* (2011) estimated that with a temperature increase of 4 °C per century, in Western Europe temperature isoclines would move northwards at a speed of 8 km per year. However, local variability in climate anomalies as a result of climate change are large. In some places temperatures may even decrease and rainfall increase. Species may either respond by physiologic and phenotypic adaptation if the climate conditions remain within the possible limits for the species, by genetic adaptation if time allows, or by migration to areas that remain or become climatically suitable (e.g. Bellard *et al.*, 2012; Cobben *et al.*, 2011; Parmesan, 2006).

The former worstcase scenarios predicting a 4° to 6°C increase in the global mean temperature (GMT) over the 21st century are becoming ever more realistic (IPCC, 2013; Kintisch, 2009). What such projected increases of 2° to even 6°C do actually imply for ecosystems and biodiversity and linked ecosystem services remains uncertain. Therefore there is an urgent need for more insight in the potential impact of future climate change on the biophysical environment.

During the past decade species distribution models (SDMs), like climate envelope models, have been developed and applied to assess the effects of climate change on the distribution of species (e.g. Bakkenes *et al.*, 2002; Guisan & Zimmermann, 2000; Heikkinen *et al.*, 2006a; Marmion *et al.*, 2009; Parviainen *et al.*, 2008; Thuiller, 2003; Thuiller *et al.*, 2008; Zimmermann & Kienast, 1999). These species distribution models are parameterized on the basis of statistical relations between a species' current distribution and environmental predictors such as bioclimatic variables. Subsequently they can be used to project the potential future distribution of suitable area where a species could occur and compare this with its current distribution. Aggregating results for more species can be used to assess potential effects on biodiversity patterns at a certain location.

Overall species range changes are the result of both range losses in areas where climate conditions become unfavourable and range expansions into areas that become suitable as a result of climate change (e.g. Thuiller *et al.*, 2006b). To what extent expansions will be realized will depend on species' dispersal capacity and landscape characteristics (Opdam & Wascher, 2004; Schippers *et al.*, 2011). Typically, in SDM's the dispersal possibilities are simplistically represented by either no-dispersal or unlimited dispersal (e.g. Araújo *et al.*, 2004; Thuiller *et al.*, 2006b), reflecting the difficulty of accurately modelling dispersal over large spatiotemporal scales. No-dispersal implies that species will only be present in the future where modelled current and future distributions overlap, while unlimited dispersal implies that all climatically suitable areas in the future are projected to be occupied by the species. Both situations are probably not very realistic, but by combining the results of these two methods the uncertainties associated with species' varying dispersion capacities can be assessed (e.g. Araújo *et al.*, 2004). Although definitions differ among publications, in general the range losses are calculated under the no-dispersal assumption, while the range expansions are calculated assuming unlimited or universal dispersal possible (e.g. Araújo *et al.*, 2004; Thuiller *et al.*, 2006b).

The objective of this study is two-fold. First we investigate the impact of increasing global mean temperature on local species richness, and more specifically local species persistence and local extinction, using a meta-analysis of

projected changes in species distributions based on results from published SDM studies. This meta-analysis allows us to generalise observed trends and to assess impacts along a broader range of temperature increases than is possible on the basis of single SDM outcomes. Second we elaborate simple dose-response meta-models that can be applied in more comprehensive local or global assessments of the effects of different pressures on biodiversity (Bakkenes *et al.*, 2008; Sala *et al.*, 2000a; ten Brink *et al.*, 2010). The GLOBIO3 modeling framework (Alkemade *et al.*, 2009) that is an example of such more comprehensive global biodiversity assessment tool includes the impact of different pressures on biodiversity. The meta-models will be used as a further improvement of the relationships between climate change and biodiversity that are currently used within the GLOBIO3 model (Alkemade *et al.*, 2011).

Material and methods

Our study is based on a systematic review of articles in which species distribution models are used to relate current and future distributions of terrestrial species to climate variables. A list of relevant keywords (see supplemental information) was used to search ISI Web of Knowledge, (version 4.10, on 03-08-2010) for papers using species distribution models to project changes in species composition and range changes. The used keywords were fine-tuned to guarantee that key publications on this subject were included (eg. Thuiller *et al.*, 2006a), resulting in a gross list of 207 publications. These publications were evaluated for their relevance and useability. Studies that did not include terrestrial species or focused on other abiotic factors instead of climate change, were omitted afterwards. Also papers that focused on exotic invading species and pests and diseases or were assessing historic and paleoecological effects were considered to be outside the scope of this study. Additionally papers were omitted if it was not possible to calculate the effect size (see below).

Calculation of effect sizes

As a consequence of climate change the potential ranges of species may shift, leading locally to turnover of species and reassembly of communities. The focus of this study is on the fraction terrestrial plant and animal species remaining at a location (Fraction Remaining Species, FRS) under projected future global mean temperature increase.

The fraction remaining species at a locality is used as an indicator for biodiversity effects (eg. Bobbink *et al.*, 2010; Gardner *et al.*, 2009) and is included in biodiversity models (Alkemade *et al.*, 2009; Alkemade *et al.*, 2011; Bakkenes *et al.*, 2006) and in policy scenario assessments (ten Brink *et al.*, 2007). It allows for combining and comparing the effects of different pressures and drivers on

biodiversity, across biomes and species groups. We calculated the fraction of remaining species (FRS) as the fraction of remaining species relative to the original species richness at a given spatial location. It is a relative species richness index between 0 (no original species present) and 1 (all original species present) that is expected to decrease with increasing global mean temperature. Of the reviewed studies most studies reported on projected shifts of ranges of different species.

To allow the calculation of the effect size publications needed to provide information on occurrence of a given species at a certain location before and after projected climate change. Several studies already aggregated the potential ranges of several species to calculate effects on species diversity in a focal area (i.e. grid cell or grid point, nature area, country, etc). For each study individual FRS effect sizes were calculated separately per biome and taxon group as these characteristics were expected to affect the impact increasing temperature will have. For the effect of biomes we followed the descriptions and locations of biomes as used within the IMAGE and GLOBIO3 integrated modelling framework (Alkemade *et al.*, 2009; Bouwman *et al.*, 2006). Because not all biomes were represented in the available publications, or with too few data points, biomes that we considered to be relatively similar were combined. This was done for tundra and wooded tundra, grassland and steppe with hot desert and tropical woodland and tropical forest.

Climate change impacts

The reference point for climate conditions differs among the different studies included in our analysis, which means that GMTI actually depends on the starting point of the original analysis. To harmonise the GMTI values for the included studies all derived GMTI values were converted to a pre-industrial reference point using Table 1. This conversion was also needed to consider species richness indicators in comparison to pre-industrial conditions, as is done in the GLOBIO3 model.

For studies reporting results from multiple climate change models, for instance based on the output from different

Table 1 Temperature increases (°C) over time as reported for the IMAGE OECD scenario.

Year	Temperature changes (°C)
1970	0.19
1975	0.17
1980	0.21
1985	0.30
1990	0.38
1995	0.51
2000	0.61
2005	0.69
2010	0.80

global circulation models (GCMs), or different SDM methods, all combinations of temperature change and SDM were included as separate data points in our analysis.

Meta-analysis

We did a meta-analysis for plant and vertebrate studies separately using the 'metafor' package (Viechtbauer, 2010) in R 2.14.0 software. We applied a random effects meta-analysis using 1 °C global mean temperature change classes (0 °C, 1-2°C, 2-3°C, 3-4°C and ≥5°C) for plants and vertebrates separately to assess the range of GMTI that has an effect on FRS in these two taxonomic groups.

Additionally linear mixed effects models were fitted for the effect size FRS and the change in global mean temperature using the 'nlme' package in R. Since it was expected that taxons respond differently and that responses of species will depend on their biome, taxon and biome were included as factors. For correction of publication bias for corresponding data points a unique paper ID was included as a random factor and each effect size value was weighted by its variance. Stepwise backward regression was based on the likelihood ratio.

Finally for application within the GLOBIO3 model we similarly fitted linear mixed effects models for FRS and GMTI for each biome separately, applying a fixed intercept of 1 (i.e. no effect if there is no temperature increase).

Results

Systematic review

Of the gross list of 207 potentially relevant studies only 21 could eventually be included in our analysis. Because studies sometimes gave different temperature increases or results based on different SDM techniques, presented

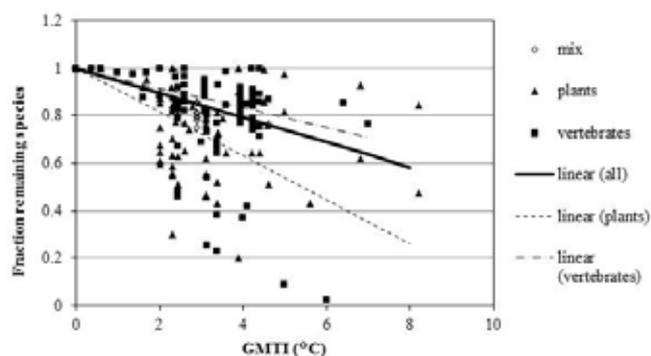


Figure 1 Relationship between global mean temperature increase and fraction of remaining species per taxon (see legend). Vertebrates, refers to other vertebrates not belonging to amphibians, birds or mammals. Mix refers to studies that included plant and vertebrate species that could not be considered separately. The bold trendline is based on all datapoints of all species groups combined.

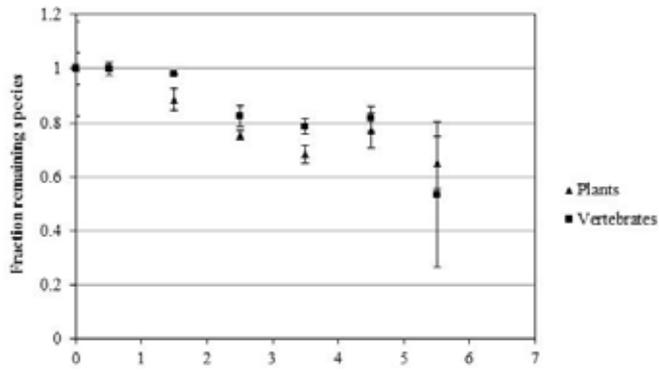


Figure 2 Pooled results of the meta-analysis for fraction remaining species per 1 °C interval of global mean temperature increase (GMTI). Triangles give the result for plants, squares for vertebrates. Error bars give the standard error for the pooled effect size. This is a visual representation of the data in Table 3 and Table 4. The interval 5-6 °C GMTI contains the effect for studies reporting > 5 °C and included GMTI values up to 8.2 °C.

results for different biomes or taxon groups or a combination of these reasons, a total of 239 data points of FRS against climate change were available (Figure 1). A diversity of regions was covered in the studies that were eventually included in our meta-analysis (Table 2). Especially studies covering regions in Europe (7) and Australia (6) were well represented. However, no studies with a focus on Asia were available.

Table 2 Studies included in the review with their focal region, number of datapoints for the effect size FRS that were included in the meta-analysis and regression analyses, and the species types included in the calculation of the effect sizes (P: Higher plants; A: Amphibians; Bi: Birds; M: Mammals; Mi: mix of taxon groups and V: other vertebrates).

No	Source	Focal region	#	P	A	Bi	M	Mi	V
1	Bakkenes et al., 2006	Europe	36	X					
2	Bässler et al., 2010	Australia	2					X	
3	Brereton et al., 1995	Switzerland	4			X	X		
4	Engler et al., 2009	Australia	8	X					
5	Fitzpatrick et al., 2008	New Zealand	3	X					
6	Gasner et al., 2010	Western hemisphere	2			X			
7	Halloy & Mark, 2003	Europe	6	X					
8	Lawler et al., 2009	Australia	44					X	
9	Lawler et al., 2010	Western hemisphere	2		X				
10	Malcolm et al., 2006	Various global, specified	24	X					X
11	Meynecke, 2004	Australia	3						X
12	Midgley et al., 2002	South Africa	2	X					
13	Pompe et al., 2008	Germany	4	X					
14	Sekercioglu et al., 2008	Western hemisphere	6			X			
15	Shoo et al., 2005	Australia	4			X			
16	Thuiller et al., 2005	Europe	5	X					
17	Thuiller et al., 2006c	Namibia	12	X					
18	Thuiller et al., 2006a	Africa	25				X		
19	Trivedi et al., 2008	Scotland	8	X					
20	Virkkala et al., 2010	Northern Europe	32			X			
21	Williams et al., 2003	North-East Australia	7						X
Total			239						

Meta-analysis

The pooled effect size derived from our meta-analysis shows that for both plant and vertebrate species the fraction remaining species decreases with increasing global mean temperature for temperature increases larger than 2 °C above pre-industrial temperature levels (Figure 2, Table 3 and Table 4). Heterogeneity was especially large for the higher GMTI intervals in plants and for most GMTI intervals in vertebrates, indicating a large variation in effects among studies. There only appeared to be publication bias in the highest GMTI interval for plants. Fail-safe numbers (Rosenthal method) indicated that a large number of studies averaging null results would need to be included to reduce the significance of the pooled effect size.

Regression analysis

All taxons showed a similar trend of decreasing FRS with increasing global mean temperature (Figure 1). If no factors (biome or taxon) are included in the model, change in global mean temperature is significantly ($p < 0.0001$) reducing FRS with a slope of 0.05 per °C (i.e. with each degree increase in global mean temperature on average across all taxons and biomes 5% of the species will disappear from a certain locality). Including biomes in the model significantly improves the model ($p < 0.0001$), accounting for the variation across different biomes. Also taxon type significantly improves the model ($p = 0.033$,

Table 3 Results of the meta-analysis for plants for different GMTI intervals

GMTI intervals (°C)	n	FRS	s.e.	CI (lb)	CI (ub)	P(FRS)	Q	P(Q)	I2 (%)	Fail safe N (Rosenthal)	Egger z	P(Egger)
All	88	0.80	0.02	0.75	0.84	<0.0001	404.84	<0.0001	73.41	133755	-0.245	0.807
0	10	1.00	0.06	0.89	1.11	1	0	1.00	0	1075	0	1
0-1	8	1.00	0.02	0.95	1.05	1	0	1.00	0	4666	0	1
1-2	12	0.89	0.04	0.80	0.97	0.0063	4.12	0.9644	0	1187	-1.543	0.123
2-3	24	0.76	0.02	0.72	0.79	<0.0001	18.38	0.7368	0	8502	-0.123	0.902
3-4	21	0.68	0.03	0.62	0.75	<0.0001	19.11	0.5145	14.02	2938	-0.350	0.726
4-5	8	0.77	0.06	0.65	0.90	0.0005	59.90	<0.0001	82.89	2365	0.533	0.594
>=5	5	0.65	0.10	0.46	0.84	0.0004	56.49	<0.0001	93.90	1185	4.915	<0.0001

Table 4 Results of the meta-analysis for vertebrates for different GMTI intervals

GMTI intervals (°C)	n	FRS	s.e.	CI (lb)	CI (ub)	P(FRS)	Q	P(Q)	I2 (%)	Fail safe N (Rosenthal)	Egger z	P(Egger)
All	129	0.84	0.02	0.80	0.88	<0.0001	6920.15	<0.0001	98.31	2679774	1.203	0.229
0	1	1.00	0.17	0.66	1.34		0.00	1.00	n.a.	12	n.a.	n.a.
0-1	21	1.00	0.01	0.99	1.01	1.00	0.01	1.00	0.00	105610	-0.037	0.971
1-2	5	0.98	0.00	0.98	0.98	<0.0001	3.54	0.47	0.00	181355	-1.197	0.231
2-3	30	0.82	0.04	0.74	0.90	<0.0001	2388.63	<0.0001	94.79	72679	n.a.	n.a.
3-4	37	0.79	0.03	0.73	0.84	<0.0001	224.06	<0.0001	94.00	155497	-1.996	0.046
4-5	32	0.81	0.04	0.73	0.90	<0.0001	370.99	<0.0001	92.74	41666	1.445	0.149
>=5	3	0.53	0.27	0.01	1.06	0.08	0.05	266.91	99.00	207	0.952	0.341

Table 5 Slope and standard error (s.e.) of the regressions per GLOBIO3 biome with a fixed intercept at FRS = 1 and corresponding number of observations included and p value for the model. Biomes are ordered from steepest slope (strongest impact) to flatter slopes (least impacts). The following biomes were combined because of lack of data in one, or both of the biomes: Tundra with Wooded tundra; Grassland and steppe with Hot desert; Tropical woodland with Tropical forest. Subsequently these biomes will receive the same equation for GLOBIO3 modeling purposes. Global gives the result for studies that had a global approach. Total gives the results for all biomes combined in one regression.

Biome	Slope Value	s.e.	n	p
Warm mixed forest	-0.1457	0.0122	17	<0.0001
Grassland and steppe	-0.1201	0.023	22	<0.001
Hot desert				
Cool coniferous forest	-0.1127	0.007	15	<0.001
Tropical woodland	-0.1075	0.0128	39	<0.0001
Tropical forest				
Savannah	-0.0775	0.0104	12	<0.001
Temperate deciduous forest	-0.071	0.008	18	<0.001
Scrubland	-0.0661	0.0072	28	<0.0001
Temperate mixed forest	-0.0487	0.0066	18	<0.001
Tundra	-0.0426	0.0045	8	<0.001
Wooded tundra				
Boreal forest	-0.0367	0.0125	48	0.005
Ice	-0.0356	0.004	8	<0.001
Mediterranean shrub	No data			
Global	-0.03	0.041	6	<0.001
Total	-0.0521	0.0047	239	<0.0001

Figure 1), showing a stronger impact of GMTI on plants than on vertebrate species, but if also the effect of biomes is included in the model, taxon information does not contribute significantly anymore. Biome specific regression equations that will be used in the GLOBIO3 modelling framework show that the effect of GMTI in general will be strongest in warm and tropical systems and smallest in cold and boreal systems (Table 5).

Discussion

The results of our meta-analysis and regression analysis support the notion that global mean temperatures in the future should not increase beyond 2 °C above pre-industrial levels. Using a meta-analysis of previously published SDMs enables analysis and generalisations of the impacts of climate change on a broad range of plant and vertebrate species, biomes and geographic regions. A recent extensive meta-analysis by Warren *et al.* (2011) also showed that impacts of climate change on a large number of ecosystems and species also strongly increases if GMTI increases beyond 2 °C. Warren *et al.* (2011) quantify many different effect and response types of ecosystems to GMTI giving much needed insight in the different effects GMTI can have on ecosystems. Our approach to calculate the same effect size across a large range of temperatures enabled us to quantify trends of the impact of increasing global mean temperature and to quantify meta-models that, in combination with the impacts of other pressures can be used in global biodiversity assessments.

The large heterogeneity observed from the meta-analysis of vertebrate species indicates a large variation in responses that are found in the underlying studies. Partly this can be explained by the large variation in taxonomic vertebrate groups that were combined under vertebrates. Data were available for different vertebrate species groups like mammals, birds, butterflies and amphibians (Table 2). Given the physiological differences between these species groups it can be expected that the impact of climate change varies. Being ectothermic species, amphibians and reptiles are projected to even profit from warming (Araújo *et al.*, 2006; Vos *et al.*, 2008) especially in cooler places. Places that previously were too cold, may now become suitable, while at the same time these species are less sensitive for higher temperatures (Araújo *et al.*, 2006). Only where this warming is associated with dry conditions, like the Iberian Peninsula, amphibian species are projected to decrease with increasing temperatures (Araújo *et al.*, 2006; Teixeira & Arntzen, 2002). Ideally vertebrate species would have been separated in different taxonomic groups, but data availability was insufficient to include these separately. Therefore to increase robustness of our analysis we grouped all vertebrate species together.

Heterogeneity was also strong at the highest GMTI interval. In fact this was an open interval including all GMTI values >5 °C, which ranged from 5.6 °C to 8.2 °C and thus naturally includes a large variation in possible impacts.

Assumptions and limitations of SDM

Bioclimatic species distribution modelling includes many uncertainties and assumptions and results must be used carefully. Especially dispersal, biotic interactions and the effects of land-use are generally acknowledged to be factors that are important to consider (Guisan & Thuiller, 2005; Heikkinen *et al.*, 2006b), as these omissions will emphasise the fundamental or potential rather than the realised niche of species (Suarez-Seoane *et al.*, 2004). For example Beale *et al.* (2008) showed that only for more extreme conditions projections of a climate envelope model performed better than a null-model.

In a study of oak species distribution Purves *et al.* (2007) found that co-occurring species can interact very differently with the environment and have different dispersal, characteristics and physiological tolerances. Thus dispersal and species interactions strongly influence range and abundance. The significance of biotic interactions in bioclimatic envelope models has also been recognised in several other studies (e.g. Araujo & Luoto, 2007; Davis *et al.*, 1998; Suttle *et al.*, 2007).

Land cover and land use variables may also explain a substantial part of species distribution patterns (Pearson *et al.*, 2004; Termansen *et al.*, 2006). A study of marshland birds in Finland showed for example that habitat availability plays a crucial role in the occurrence of marshland birds (Virkkala *et al.*, 2005), and edaphic variables significantly improved the quality of predictions for *Acer campestre* (Coudun *et al.*, 2006). Nevertheless, Thuiller *et al.* (2004) argued that at the European scale, land cover is mainly driven by climate and land cover may improve the explanatory but not the predictive power of bioclimatic models.

Co-occurring and interdependent species may respond differently as a consequence of climate change. Future potential ranges in that case thus not only depend on the potential range of the focal species, but also that of other species. As a consequence modelling studies that ignore this potential mismatch may underestimate the effect of climate change (Binder & Ellis, 2008; Schweiger *et al.*, 2008; Williams & Jackson, 2007). In the reviewed studies this interdependence was only taken into consideration in a limited number of studies (e.g. Binder & Ellis, 2008; Schweiger *et al.*, 2008), where it has shown to significantly reduce the future potential range. These studies were not included in the meta-analysis because it was not possible to calculate the desired effect size.

A study of 98 butterfly species in Finland revealed that the inclusion of species traits such as body size, breeding habitat and mobility can have a strong impact on the performance of bioclimatic envelope models (Poyry *et al.*, 2008). Large butterfly species (>50 mm in wing span) were modelled more accurately than small ones. Species inhabiting mires were difficult to model, whereas the models for species inhabiting rocky outcrops, field verges and open fells were more accurate. Furthermore, the geographical attributes of a species may significantly influence the behaviour and uncertainty of species–climate models. Luoto *et al.* (2005) showed for example that model accuracy for butterflies increased with spatial autocorrelation of the species. The distribution of species at the margin of their range or with low prevalence were easier to predict than widespread species, and species with clumped distributions were easier to construct good models for than scattered dispersed species.

Pearson *et al.* (2004) demonstrate that the search for environmental correlates with species' distributions must be addressed at an appropriate spatial scale. Their study contributes to the mounting evidence that hierarchical schemes are characteristic of ecological systems. Trivedi *et al.* (2008) showed that the resolution used for calibrating the species–climate relationship actually has an important effect on the results of projections of future distributions under climate change. Projections under low (+1.7 °C) or high (+3.3 °C) climate change scenarios showed that models based on fine resolution (local scale, 50 m x 50 m) predicted seven or eight out of 10 species to disappear from a mountain range in Scotland. The projections based on coarser resolutions (macro scale) only predicted such loss for one species. Models using large scale resolution thus appear to overestimate the ability of alpine species to cope with raising temperatures. Also Luoto and Heikkinen (2008) included topographic variation to the bioclimatic models and showed that this improved the predictive accuracy for 86% of the 100 butterfly species. These climate-topography models tended to especially change the predictions with regard to mountainous regions, where they predicted only half of the species losses, while they doubled the predicted losses in the flatland regions.

It has been suggested that accuracy of bioclimatic envelope models can be improved by using (1) an approach that explores the consensus between different models (Araujo & New, 2007); (2) a local regression analysis, which allows the relationship under study to vary in space, rather than conventional global regression analysis (Foody, 2008), (3) species-specific climate variables (Heikkinen *et al.*, 2006c); and (4) the integration of climate and land cover information at smaller scales (<40 km resolution) (Luoto *et al.*, 2007).

Spatial scale

Differences in spatial scale are an important source of variability in model outcomes. It appears that models on coarser spatial scales fail to represent the local topographic variability and habitat heterogeneity (Gillingham *et al.*, 2012; Luoto & Heikkinen, 2008; Randin *et al.*, 2009). For applications that need to project current distributions of single species, or look at small spatial scales, the accuracy issues appear to be a bigger problem than for assessments of future global biodiversity impacts of climate change (e.g. Parmesan *et al.*, 2005; Thuiller *et al.*, 2004, across Europe).

Time dependency

In our analysis we only consider the effect of changing mean global temperature, but we neglect the time interval in which this change materialises. The impact will most likely be stronger if changes occur over shorter time intervals, while the same temperature increase that takes a longer time period may allow species locally to adapt to changes, or keep pace with their moving range. Among the studies included in our meta-analysis there are large differences in these time intervals for similar GMT increase. This is likely an important source of variation among studies, contributing to the observed heterogeneity of the meta model.

Supporting policy making and conservation planning

Currently potential effects of climate change on species distributions have not or only partly been included in protocols for selection and planning of conservation areas (e.g. Araújo *et al.*, 2004; del Barrio *et al.*, 2006; Wilson & Piper, 2008), while reserves will not necessarily be able to adequately protect species' long term persistence (Araújo *et al.*, 2004; del Barrio *et al.*, 2006). The same is true for selection of habitats within the EU habitat directive (Normand *et al.*, 2007) and Natura 2000 sites (e.g. Vos *et al.*, 2008), that more or less assume that species distributions and habitat suitability are static.

Conclusion

Notwithstanding the uncertainties associated with SDMs most of the reviewed studies showed similar trends across taxonomic groups and biomes. The meta-model based on outputs and projections of future distributions under climate change from bioclimatic species distribution models can readily be used for informed policy making and global biodiversity assessments. In the meantime models should be further improved to be able to direct more specific policies targeted at halting global loss of species.

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Annex: Supplemental information: Selection of reviewed sources

Terms used in the query for relevant literature in Web of Knowledge 4.10 (03/08/2010):

Topic=((climat* SAME change*) OR (temperature SAME change*) OR (temperature SAME increase) OR (global SAME change*) OR (global SAME warming) OR (climat* SAME warming)) AND Topic=(biodiversity OR (diversity SAME species) OR (species SAME richness*) OR (species SAME distribution*) OR (species SAME abundance*) OR (species SAME occurrence*) OR (species SAME turnover) OR (species SAME loss*) OR (species SAME gain*) OR (species SAME composition) OR (species SAME assemblage*)) AND Topic=("bioclimat* model*" OR "niche* model*" OR "climat* model*" OR "distribution model*" OR "habitat model*" OR "ecologic* model*" OR "occurrence model*" OR "species distribution model*" OR "future SAME distribution*" OR "model* distribution*" OR "model* range*" OR "climat* envelope*" OR "envelope* model*" OR (climat* SAME scenario)).

Colofon

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Keywords: global mean temperature increase, fraction remaining species, species richness, terrestrial biodiversity; species distribution models; meta-analysis; GLOBIO3

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